Predation Risk as a Driving Force for Phenotypic Assortment: A Cross-Population Comparison

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Summary

Frequency dependent predation has been proposed as a general mechanism driving the phenotypic assortment of social groups via the 'oddity effect', which occurs when the presence of odd individuals in a group allows a predator to fixate on a single prey item increasing the predator's attack to kill ratio. The generality of the oddity effect has however been debated and there has not previously been an ecological assessment of the role of predation risk in driving the phenotypic assortment of social groups. Here, we compare levels of body length assortment of social groups between populations of the Trinidadian guppy (*Poecilia reticulata*) that experience differences in predation risk. As predicted by the oddity effect hypothesis, we observe phenotypic assortment by body length to be greater under high predation risk. However, we also found that a number of low predation populations were also significantly assorted by body length, suggesting that other mechanisms may also have a role to play.

Keywords: Confusion effect, frequency dependent selection, guppy, oddity effect, *Poecilia reticulata*.

Introduction

Across a broad range of taxa social groups are assorted by phenotypic traits such as body size, species and sex (see Krause & Ruxton 2002 for a review). A general mechanism proposed to drive this phenotypic assortment is frequency dependent predation with odd individuals in a group suffering an increased risk of predation due to the 'oddity effect' (Landeau & Terborgh 1986; Ohguchi 1978; Theodorakis 1989). The oddity effect occurs when the presence of odd individuals in a group allows a predator to fixate on a single prey item, overcoming the 'confusion effect' and increasing the predator's attack-to-kill ratio (Krakauer 1995; Tosh et al. 2006). The confusion effect occurs across taxonomic groups including fish, mammals and reptiles (Landeau & Terborgh 1986; Neill & Cullen 1974; Ohguchi 1978; Schradin 2000; Theodorakis 1989) and previous work has generally shown that a predator's success is reduced when attacking homogeneous-looking groups (see Krause & Ruxton 2002 for a review). The oddity effect has been proposed is a major force driving evolution, so powerful that it can result in the convergence of phenotypic traits (Greenwood 1985) and may result in the extinction of rare phenotypes or species from communities. For example, recent work on corral reef assemblages has demonstrated that rare species are preferentially taken by predators (Almany et al. 2007), which may lead to reduced species diversity in areas of high predation risk (Almany & Webster 2004). However, whilst the oddity effect has received a lot of attention in the literature there is a paucity of studies evaluating the importance of this selective force in wild populations.

Much of the work on the role of the oddity effect in driving phenotypic assortment comes from work on freshwater fish with some of the most convincing evidence from experimental work looking at predator prey choice. For example, a number of studies have presented predators with groups of prey that differed in abundance of different

phenotypes, and demonstrated frequency dependent predation with predators showing a preference for the rare prey type (Ohguchi 1978). The most commonly cited of these include an experiment by Theodorakis (1989) in which when predatory bass (*Micropterus salmoides*) were presented with shoals of minnows that were dominated by one size category, the minority size was taken more often than would be predicted by chance. In a similar study Landeau and Terborgh (1986) showed that large mouth bass (*M. salmoides*) were more successful at predating shoals of minnows (*Hybognathus nuchalis*) when the shoals contained odd individuals (created by dying fish blue to adjust the frequency of phenotypes in a group). These results, however, are far from universal. For example, there are instances reported when predators show a preference for the common prey type (Fullick & Greenwood 1979) and where prey preference is independent on their frequency in a group (Fitzgibbon 1990).

In an attempt to tease apart the role of predation risk in driving phenotypic assortment a number of studies have examined the behaviour of prey under predation threat. For example, Krause and Godin (1994) reported active preferences for conspecifics of a similar size that increased in magnitude under predation threat. Other experiments have examined the behaviour of odd fish in a shoal and suggest that odd individuals show more threat sensitive behaviour under predation risk. For example, Peuhkuri (1997; 1998) found that feeding activity of large fish (*Gasterosteus aculeatus*) was sensitive to the degree of assortment of the group with large fish decreasing foraging when they were the odd phenotype in the group. In contrast small fish showed no such sensitivity. In a similar study Allan and Pitcher (1986) examined the response of mixed species shoals to a simulated predation attack finding that shoals segregated into single species groups, suggesting that the oddity effect may have an important role to play. Once again however, these results are not universal and Krause (1994),

for example, found that simulated predation risk did not change group composition of fish shoals with regards to body length.

From a review of the literature it is clear that experimental evidence for the oddity effect remains inconclusive. In much of the published literature more attention has been given to studies that report results in favour of the oddity effect (e.g. Landeau & Terborgh 1986; Theodorakis 1989), leading some authors to suggest that there is a "premature belief in the pervasiveness of the oddity effect in nature" (Krause & Ruxton 2002). Moreover, much of the work examining the role of predation risk in driving phenotypic assortment has been conducted under laboratory conditions and there is a need to evaluate the importance of this selective force in wild populations. In the current study we examine the role of predation risk in driving phenotypic assortment by comparing the degree of body size assortment of social groups sampled from 10 wild populations of Trinidadian guppies (*Poecilia reticulata*) that experience differing levels of predation.

The guppy system in Trinidad offers a rare opportunity to compare populations that live under different ecological conditions, particularly that differ in predation risk (Magurran 2005). In the Northern mountain range predatory fish assemblages change along an elevation gradient as waterfalls restrict the upstream movement of major predators, leaving headwaters relatively predator free (Magurran 2005). This allows for comparative studies of populations that differ in the predation risk they experience. Early pioneering work in Trinidad compared the degree of social behaviour between populations, providing compelling evidence for the role of predation risk in selecting for group living (Magurran & Seghers 1991; Seghers 1974). More recent work demonstrates that under high predation groups are assorted based on body size and that this assortment is in part due to active choice (Croft et al. 2003), making the

guppy particularly suited to the present study. In accordance with the oddity effect hypothesis we predict that populations living under high predation risk will form social groups that are more assorted by body length than populations living under low predation risk. This study provides a first and much needed ecological assessment of the role of predation risk in driving phenotypic assortment.

Methods

A total of 10 populations were sampled in the Northern Mountain Range of Trinidad, five that experience high predation risk and five that experience low predation risk (see Table 1). Areas of high predation were defined by the presence of the major guppy predators *Crenicichla frenata*, *Aequidens pulcher*, and *Hoplias malabaricus* (Endler 1978; Magurran & Seghers 1990; Seghers 1974). Low predation areas contained only the minor predators *Rivulus hartii* (known to prey preferentially on juveniles and small guppies (Rodd & Reznick 1991; Seghers 1973)) and the freshwater prawn, *Macrobrachium spp*. Six of the rivers were sampled over a 6-week period (May and June) in 2004 and the remaining four of the rivers were sampled over a 6-week period (May and June) in 2008 (see Table 1). The sampling design was balanced in that the same number of high and low predation rivers were sampled in a given year. In addition to sampling naturally established populations, we utilised a previous transplant of guppies carried out by Haskins in 1957 (reported by Magurran et al. 1992; Shaw et al. 1991). Haskins transplanted approximately 200 adult guppies from the Arima River (high predation) to a previously guppy-free and low predation risk location in the upper Turure River. Previous work on the transplant population has shown that behaviour has been modified by selection in accordance with the reduction in predation risk (Magurran et al. 1992).

During sampling guppy shoals (defined as a group of fish with less than four body-lengths of distance between individuals (see Croft et al. 2003)) were caught by two observers from each population using a beach seine net (190 cm x 115 cm, mesh size=3mm) between 10:00 and 16:00 hours. Shoals were only considered for analysis when both observers were satisfied that the entire shoal had been captured. To provide a representative sample of each population, a minimum of 25 shoals were captured from a minimum of five different pools in each of the rivers (the only exception to this was the Yara low predation population where only one pool could be sampled), and from different locations in each pool. The body length (total length measured to the nearest mm) of all fish capture in each shoal was recorded. To prevent multiple captures of the same individuals, sampled shoals were not released back into the river until all shoals had been captured.

Analysis

As a measure of phenotypic assortment we use the shoal coefficient of variation (COV) of body length, which was calculated for each shoal captured and we refer to this measure as the degree of *absolute assortment*. To determine if shoals were more assorted than we would have expected if fish associated randomly with regard to body size we calculated the *expected assortment* for each shoal assuming random interactions between individuals within a river. This was calculated using a constrained randomization test in which individuals from all captured shoals within a river were pooled and shoals (consisting of the number of individuals in a natural shoal from the respective river) were then selected at random and the COV of body length calculated for each re-sampled shoal. Ten thousand random shoals were generated for each shoal captured and the average COV of body length calculated for

each shoal as the value of *expected assortment*. Finally, to provide a single variable that allowed us to compare the degree of non-random assortment between rivers for each shoal we calculated the degree of *relative assortment* for each shoal as the proportion of iterations in the randomisation that produced a COV of less than or equal to the observed COV. Given that the value of relative assortment is a proportion we transformed the data using an arcsine square root transformation.

To examine the degree of phenotypic assortment by body length within rivers we used a one sample t-test for each river to compare the difference between the observed (*absolute assortment* minus *expected assortment*) and expected values of assortment to a value of zero (i.e. the expected value assuming no assortment). We used a nested general linear model (GLM) to assess if shoal assortment differed between habitat types (high and low predation risk) and/or among rivers. Relative assortment was entered as our dependent variable and predation risk and river nested within predation risk were entered as our fixed effects. All statistical analyses were carried out in SPSS version 14.0. Where appropriate we used a Bonferroni correction to control for multiple testing.

Results

Body length assortment within rivers

Significant body length assortment was observed in all five populations living under high predation risk (see Figure 1a). Interestingly, significant size assortment was also seen in two of the low predation populations Naranjo and Yara (see Figure 1b).

Differences in assortment between high and low predation:

We found significant differences in relative assortment between high and low predation risk, with shoals in high predation being significantly more assorted than shoals in low predation ($F_{1,325}$=10.283, P=0.001, see Figure 2). There was also a significant difference in relative assortment among sites ($F_{8,325}$=2.270, P=0. 023, see Figure 1). When we made a direct comparison between the degree of relative assortment between the population transplanted from high to low predation (Turure mean(± 1 SE)=0.60±0.04) and the original founder population (Arima mean(± 1 SE)=0.43±0.02) assortment was significantly reduced in the transplanted population living under low predation (t-test t_{75}=2.64, P=0.010).

Discussion:

Our results demonstrate that predation risk is an important factor driving phenotypic assortment in wild populations. By comparing levels of phenotypic assortment between populations that experience differences in predation risk we were able to show that the magnitude of assortment in comparison to what would be expected by random interactions is greater under high predation risk than under low predation risk as predicted by the oddity effect hypothesis.

The comparative approach is a powerful tool to emphasise the role of ecological variables in driving population differences in behaviour. Some of the earliest and most significant applications of this approach investigated the role of predation risk in driving group living with a number of studies finding that species that live under high predation risk form larger groups (Crook 1965; Jarman 1974; Seghers 1974). In the current investigation we extend this analysis to look at the composition of social

groups that experience differences in predation risk. In accordance with theoretical predictions stemming from the oddity effect hypothesis, under high predation shoals of fish were more assorted than shoals from low predation rivers relative to what we would expect if interactions occurred at random. This result could be due to predators selectively removing odd individuals from shoals via frequency dependent predation. However, given the dynamic nature of the fission fusion system with individuals exchanging shoals over a time scale of minutes (Croft et al. 2003) and that previous work has shown that shoal assortment in guppies is in part driven by active choice (Croft et al. 2003), it is likely that observed patterns are based on some sort of active choice of shoal membership based on body length. Future work comparing the shoal choice behaviour of individuals that experience different predation regimes would be greatly rewarding.

Whilst the comparative approach provides a powerful tool it does have its limitations (Clutton-Brock & Harvey 1979; Gould & Lewontin 1979) in particular associations between ecological variables may confound the results of a comparative study. In guppy populations in the Northern Mountain Range of Trinidad habitat differences predation risk are often correlated with productivity (Grether et al. 2001; Reznick et al. 2001). High predation rivers tend to have higher levels of productivity than low predation rivers as the forest canopy is usually less dense in these habitats (Grether et al. 2001; Reznick et al. 2001). This combined with the fact that low predation rivers usually have a higher density of fish leads to higher competition between individuals for food under low predation which is known to be a strong selective force in guppies (Arendt & Reznick 2005; Reznick et al. 2001). Competition for food has been proposed previously as a mechanism selecting for size assortative shoaling in fish (Ranta et al. 1994). However, the food competition hypothesis for body length

assortment predicts that assortment will be greater under intense competition for food, which in the case of the current investigation is more likely to occur in low predation populations. In support of predation risk being the major driving force for phenotypic assortment we see a reversal of this predicted pattern.

One of the strengths of the comparative approach is that it can be used to indentify general ecological and evolutionary trends however, it does this using correlational evidence which makes it difficult to invoke cause-effect relationships. More direct evidence for the link between predation risk and behaviour can be gained through transplant experiments in which predators and/or their prey are moved between habitats. In the current investigation we make use of a historical transplant experiment in which fish were moved from high to a low predation habitat (see methods for details). Previous work on the transplanted population has shown that behaviour has been modified by selection in accordance with the reduction in predation risk (Magurran et al. 1992). Our results show that shoal assortment by body length is reduced in the transplanted population providing compelling support for the importance of predation risk in selecting for phenotypic assortment.

Whilst our results provide strong support for the role of predation risk in driving the phenotypic assortment of social groups, we observed significant variation among rivers independent of predation risk and two populations living under low predation risk had social groups that were significantly assorted by body size. Taken together these results suggest that factors in addition to predation risk may contribute to assortative grouping by body size. Two alternative hypotheses 1 have been proposed in the literature that may drive body length assortment of social groups under low predation risk. Firstly, as discussed above avoidance of competition for food may select for assortative grouping by body size in these low predation risk populations

with more intense competition for food. Furthermore, variation in productivity among rivers independent of predation risk may contribute to the among river differences in body length assortment. A second mechanism that may contribute to the body length assortment is that proposed by the activity budget hypothesis (Conradt 1998; Ruckstuhl 1998). Individuals of a different size may have different activity budgets, leading some authors to propose the activity budget hypothesis to explain group assortment, particularly between mixed sexed groups where there is sexual dimorphism in body size (Conradt 1998; Ruckstuhl 1998). In fish, optimal foraging rates and swimming speeds are size dependent (Beamish 1978; Hjelm & Persson 2001) and individuals in a group of others of dissimilar body length may be forced to travel and forage at sub-optimal speeds, potentially incurring an energetic cost which may contribute selection for group assortment by body size in shoaling fish (Ruckstuhl 2007). Experimentally testing the importance of competition and activity synchrony as mechanisms driving phenotypic assortment in natural populations, particularly under low predation risk, provides an exciting challenge for future research.

In conclusion our results provide compelling evidence for the role of predation risk and the oddity effect in driving phenotypic assortment by body size. However, our results also suggest that other factors may have an important role to play and highlights the need for future work on this phenomenon in wild populations.

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References:

Allan, J. R. & Pitcher, T. J. 1986 Species segregation during predator evasion in cyprinid fish shoals. *Freshwater Biology* **16**, 653-659.

Almany, G. R., Peacock, L. F., Syms, C., McCormick, M. I. & Jones, G. P. 2007 Predators target rare prey in coral reef fish assemblages. *Oecologia* **152**, 751-761.

Almany, G. R. & Webster, M. S. 2004 Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* **85**, 2933-2937.

Arendt, J. D. & Reznick, D. N. 2005 Evolution of juvenile growth rates in female guppies (Poecilia reticulata): predator regime or resource level? *Proceedings of the Royal Society B-Biological Sciences* **272**, 333-337.

Beamish, F. W. H. 1978 Swimming capacity. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar & J. D. Randall), pp. 101–187. New York: Academic Press Inc.

Clutton-Brock, T. H. & Harvey, P. H. 1979 Comparison and adaptation. *Proceedings of the Royal Society of London Series B-Biological Sciences* **205**, 547-565.

Conradt, L. 1998 Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1359-1363.

Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I. & Krause, J. 2003 Mechanisms underlying

shoal composition in the Trinidadian guppy (*Poecilia reticulata*). *Oikos* **100**, 429-438.

Crook, J. H. 1965 The adaptive significance of avian social organizations. *Symposia of the Zoological Society of London*, 181-218.

Endler, J. A. 1978 A predators view of animal colour patterns. *Evolutionary Biology* **11**, 319-364.

Fitzgibbon, C. D. 1990 Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour* **39**, 1116-1126.

Fullick, T. G. & Greenwood, J. J. D. 1979 Frequency dependent food selection in relation to two models. *The American Naturalist* **113**, 762-765.

Gould, S. J. & Lewontin, R. C. 1979 Spandrels of San-Marco and the Panglossian paradigm - a critique of the adaptationist program. *Proceedings of the Royal Society of London Series B-Biological Sciences* **205**, 581-598.

Greenwood, J. J. D. 1985 Frequency-dependent selection by seed-predators. *Oikos* **44**, 195-210.

Grether, G. F., Millie, D. F., Bryant, M. J., Reznick, D. N. & Mayea, W. 2001 Rain forest canopy cover, resource availability, and life history evolution in guppies. *Ecology* **82**, 1546-1559.

Hjelm, J. & Persson, L. 2001 Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. *Oikos* **95**, 520-532.

Jarman, P. J. 1974 The social organisation of antelope in relation to their ecology. *Behaviour* **48**, 215–267.

Krakauer, D. C. 1995 Groups confuse predators by exploiting perceptual bottlenecks - a connectionist model of the confusion effect. *Behavioral Ecology and Sociobiology* **36**, 421-429.

Krause, J. 1994 The influence of food competition and predation risk on size-assortative shoaling in juvenile chub (*Leuciscus cephalus*). *Ethology* **96**, 105-116.

Krause, J. & Godin, J. G. J. 1994 Shoal choice in the banded killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae) - Effects of predation risk, fish size, species composition and size of shoals. *Ethology* **98**, 128-136.

Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford: Oxford University Press.

Landeau, L. & Terborgh, J. 1986 Oddity and the confusion effect in predation. *Animal Behaviour* **34**, 1372-1380.

Magurran, A. E. 2005 *Evolutionary ecology: The Trinidadian guppy*. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press.

Magurran, A. E. & Seghers, B. H. 1990 Population differences in the schooling behaviour of newborn guppies, *Poecilia reticulata*. *Ethology* **84**, 334-342.

Magurran, A. E. & Seghers, B. H. 1991 Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour* **118**, 214-234.

Magurran, A. E., Seghers, B. H., Carvalho, G. R. & Shaw, P. W. 1992 Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of antipredator behaviour in the wild. *Proceedings of the Royal Society of London Series B-Biological Sciences* **248**, 117-122.

Neill, S. R., St.J. & Cullen, J. M. 1974 Experiments on whether schooling by their prey affects the hunting behavoiur of cephalopods and fish predators. *Journal of Zoology*. **172**, 549-569.

Ohguchi, O. 1978 Experiments on the selection against colour oddity of water fleas by three-spined stickelbacks. *Zeitschrift fur Tierpsychologie* **47**, 254-67.

Peuhkuri, N. 1997 Size-assortative shoaling in fish: The effect of oddity on foraging behaviour. *Animal Behaviour* **54**, 271-278.

Peuhkuri, N. 1998 Shoal composition, body size and foraging in sticklebacks. *Behavioral Ecology and Sociobiology* **43**, 333-337.

Peuhkuri, N. 1999 Size-assorted fish shoals and the majority's choice. *Behavioral Ecology and Sociobiology* **46**, 307-312.

Ranta, E. & Lindström, K. 1990 Assortative schooling in three-spined sticklebacks. *Annales Zoologici Fennici* **27**, 67-75.

Ranta, E., Peuhkuri, N. & Laurila, A. 1994 A theoretical exploration of antipredatory and foraging factors promoting phenotype-assorted fish schools. *Ecoscience* **1**, 99-106.

Reznick, D., Butler, M. J. & Rodd, H. 2001 Life-history evolution in guppies. VII. The comparative ecology of high - and low-predation enviroments. *The American Naturalist* **157**, 12-26.

Rodd, F. H. & Reznick, D. N. 1991 Life-history evolution in guppies .3. The impact of prawn predation on guppy life histories. *Oikos* **62**, 13-19.

Ruckstuhl, K. E. 1998 Foraging behaviour and sexual segregation in bighorn sheep. *Animal Behaviour* **56**, 99-106.

Ruckstuhl, K. E. 2007 Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology* **47**, 245 - 257.

Schradin, C. 2000 Confusion effect in a reptilian and a primate predator. *Ethology* **106**, 691-700.

Seghers, B. H. 1973 An analysis of geographic variation in the anti-predator adaptations of the Guppy, *Poecilia reticulata*. In *Zoology*: The University of British Columbia.

Seghers, B. H. 1974 Schooling behaviour in the guppy (*Poecilia reticulata*): An evolutionary response to predation. *Evolution* **28**, 486-489.

Shaw, P. W., Carvalho, G. R., Magurran, A. E. & Seghers, B. H. 1991 Population differentiation in Trinidadian guppies (*Poecilia reticulata*) - patterns and problems. *Journal of Fish Biology* **39**, 203-209.

Theodorakis, C. W. 1989 Size segregation and the effects of oddity on predation risk in minnow schools. *Animal Behaviour* **38**, 496-502.

Tosh, C. R., Jackson, A. L. & Ruxton, G. D. 2006 The confusion effect in predatory neural networks. *American Naturalist* **167**, E52-E65.

Table 1: Rivers sampled in the study, with grid references, classification as high or low predation, the number shoals caught per river and the total number of fish sampled per river.

River	Predation	Year Sampled	Grid reference		Number shoal captures	Total fish captures
			N	W		
Turure	Low	2004	10º41´	61º10´	40	273
Naranjo	Low	2004	10º41´	61º14´	35	446
Paria	Low	2004	10º45´	61º16´	38	374
Yarra	Low	2008	10º45´	61º20´	25	101
Marianne	Low	2008	10º45´	61º17	29	114
Arima	High	2004	10º41´	61º17´	33	460
Aripo	High	2004	10º40´	61º14´	38	433
Guanapo	High	2004	10º40´	61º15´	33	348
Tacarigua	High	2008	10º41´	61º22´	30	302
Quare	High	2008	10º40´	61º12´	30	290

Figure 1: Patterns of body length assortment (mean±(1SE) absolute-expected assortment) within high predation risk (a) and low predation risk rivers (b). Also shown are the results of one sample t tests comparing the difference in assortment (*absolute assortment-expected assortment*) to the expected value of 0. *=results are significant at P<0.05 after Bonferoni correction and **= are significant at P<0.01 after Bonferoni correction.

Figure 2: Patterns of body length assortment across high and low predation risk rivers showing the grand mean (± 1 SE) *relative assortment*. 1=high predation risk and 2=low predation risk.

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